

LETTER

Parasites lost – do invaders miss the boat or drown on arrival?

Catriona J. MacLeod,^{1*} Adrian M. Paterson,² Daniel M. Tompkins¹ and Richard P. Duncan³

¹Landcare Research, Private Bag 1930, Dunedin 9054, New Zealand

²Department of Ecology, Lincoln University, PO Box 84, Lincoln 7647, New Zealand

³Bio-Protection Research Centre, Lincoln University, PO Box 84, Lincoln 7647, New Zealand

*Correspondence:

E-mail: macleodc@

landcareresearch.co.nz

Abstract

Host species that colonize new regions often lose parasite species. Using population arrival and establishment data for New Zealand's introduced bird species and their ectoparasitic chewing lice species, we test the relative importance of different processes and mechanisms in causing parasite species loss. Few lice failed to arrive in New Zealand with their hosts due to being missed by chance in the sample of hosts from the original population (missing the boat). Rather, most lice were absent because their hosts or the parasite themselves failed to establish populations in their new environment. Given they arrived and their host established, parasite persistence was more strongly related to factors associated with transmission efficiency (number of host individuals introduced, host body size, host sociality and parasite suborder) than parasite propagule pressure and aggregation. Such insights into parasite success are invaluable to both understanding and managing their impact.

Keywords

Aggregation, chewing lice, ectoparasites, introduced birds, introduction success, propagule pressure, sorting events, transmission efficiency.

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INTRODUCTION

Hosts often lose parasite species when they are introduced to or colonize new regions ('sorting events'; Dobson & May 1986, 1991; Dove 2000; Torchin *et al.* 2002, 2003; Drake 2003). Whether a parasite species successfully colonizes a new region or not, following introduction of its host, is governed by three processes. First, the parasite must be present on individuals in the host founder populations; it may fail simply because parasites are aggregated across host individuals and, by chance, those host individuals in the founding populations may not have been infected with the parasite (termed 'missing the boat'; Dobson & May 1986; Paterson & Gray 1997; Paterson *et al.* 1999; Torchin *et al.* 2003). Second, the parasite's host species must persist in the new region (assuming there are no alternative hosts in the new range); if infected hosts arrive but fail to establish, the parasite will also fail (termed 'sinking with the boat'). Finally, if infected hosts arrive and persist, the parasite must likewise persist and not fail for other reasons (termed, in keeping with the hosts-as-boats theme, 'lost overboard').

For parasite species that arrive with a host, and where that host persists in the new region, several mechanisms

have been proposed to explain why parasites might subsequently fail (be lost overboard). First, one or more additional host species that are required in the parasite's lifecycle may be absent at the new locality (Dobson & May 1986; Torchin *et al.* 2003). Second, parasite transmission among host individuals at the new locality may be insufficient to offset parasite losses when hosts die (Paterson *et al.* 1999, 2003). Proposed host factors contributing to insufficient transmission include small founding populations, high mortality rates and low levels of social interaction (Gill 1990; Ewald 1994; Rózsa 1997; Rózsa *et al.* 1996; Rékási *et al.* 1997; Paterson *et al.* 1999, 2003). Proposed parasite factors contributing to insufficient transmission include low vagility and high host-specificity (reducing the pool of 'suitable' hosts in the new locality; Clayton *et al.* 2003). Third, parasite persistence is likely to be influenced by both the number of individual parasites introduced ('propagule pressure'; Lockwood *et al.* 2005) and their distribution among host individuals, with highly aggregated or low numbers of parasites more likely to be lost through stochastic processes (Poulin 2007).

Understanding why host species lose or retain their parasites on colonizing new regions is important for two

reasons. First, the invasive success of many host species is often attributed, at least in part, to release from the regulatory effects of parasites in their native range (Keane & Crawley 2002; Shea & Chesson 2002; but also see Colautti *et al.* 2004). Such 'enemy release' may allow introduced hosts that lose their parasites to attain unnaturally high densities and to become 'pests' in new locations, with often far-reaching ecological consequences (Vitousek *et al.* 1997; Wilcove *et al.* 1998; Keane & Crawley 2002). Second, many parasite species can themselves cause harm outside their native range (Daszak *et al.* 2000; Cleaveland *et al.* 2002), and understanding how parasites succeed in colonizing new regions is central to mitigating their spread and impact. Despite this, we have little understanding of which processes and mechanisms are important in determining the success of parasites in colonizing new regions following host introduction. This is because data on the host and parasite founding populations, critical to distinguishing among potential causes of parasite loss, are generally lacking (Paterson *et al.* 2003). In this study, we present the first analysis of a suite of processes and mechanisms that potentially influence whether a parasite colonizes a new region following introduction of its host, making use of a host/parasite system for which data on the host founding populations are uniquely available: New Zealand's introduced birds and their ectoparasitic chewing lice.

Ectoparasitic lice are well suited to investigations of parasite sorting events because, relative to endoparasites, ectoparasites have a low risk of being missed upon host examination (Cooper & Anwar 2001) and chewing lice, in particular, are relatively easy to collect and identify. In addition, being directly transmitted parasites for which the body of the host is the habitat, lice are relatively unaffected by external environmental variables that can strongly influence the persistence of other parasites (Harvell *et al.* 2002). Introduced birds to New Zealand are equally well suited as hosts for such an investigation because there are detailed historical data on the size of the founding populations for most species (Veltman *et al.* 1996; Duncan 1997; Duncan *et al.* 1999). These hosts and their parasites have also been well studied in their native range. Hence, this is an ideal model system for such an investigation. We thus use these data to estimate the relative importance of 'missing the boat', 'sinking with the boat' and being 'lost overboard' in determining whether the parasitic chewing lice of birds introduced to New Zealand succeeded in establishing. For lice that arrived with their host species, and where that host established in New Zealand, we further identify the mechanisms that determine whether a parasite species persisted or not in the new locality. More specifically, we tested the relative importance of propagule pressure, parasite aggregation and transmission efficiency in determining parasite species persistence.

METHODS

Data collection

We obtained data on the number of individuals of bird species introduced to New Zealand (Table 1) from Veltman *et al.* (1996), Duncan (1997) and Duncan *et al.* (1999). For a subset of these bird species, we obtained data on chewing lice infestations from both the global range of the species (excluding New Zealand; 45 species) and from UK/Ireland (from where most of New Zealand's introduced bird populations were sourced; 31 species), using data from a collection of notebooks and slides compiled by Richard Meinertzhagen in the early to mid 1900s, and housed at the Natural History Museum, London, UK (Table 1). With UK/Ireland being a relatively close climate match to New Zealand (MacLeod *et al.* 2009), if there was an important influence of environmental variables on the probability of louse persistence it should manifest as differences between these two datasets. Bird species were included only if the numbers of individuals introduced to New Zealand were known, and if data from 10 or more individuals had been sampled for chewing lice (to reduce the probability of non-detection of lice due to small samples).

Meinertzhagen's notebooks provided data on the number of individuals in chewing louse families or genera that he had identified on individual host specimens, along with records of host specimens that he had sampled but that lacked chewing lice. In total, the notebooks yielded data on chewing lice infections for 2741 host individuals of the 45 bird species in their native ranges (Table 1). To confirm Meinertzhagen's identifications, we cross-referenced the notebook data with 314 specimen slides from 22 bird species that were held in an associated collection at the Natural History Museum, London, UK.

Meinertzhagen's notebooks also recorded information on the location where individual host specimens were collected, which enabled us to identify host individuals collected in UK/Ireland. Parasite family or genus level records in the notebooks were cross-referenced to the slide collection where possible to enable identification to the genus or species level. Where no further information was available in the slide collection, records from the global and UK/Ireland datasets were cross-referenced with the world and British chewing lice checklists respectively (Steel *et al.* 1964; Redgate 1996; Price *et al.* 2003) to determine whether they could be attributed to a particular genus or species. Because many records could be identified only to genus or family, we carried out our analyses at two taxonomic levels: at the genus-level and, for the subset of records identified to species, at the species-level. (For records where the genus or species level identifications could not be ascertained the higher taxonomic level was retained in the analyses; see Appendices S1–S4.)

Host species	Introduced to New Zealand	No. host individuals sampled for parasites		Established in NZ
		Global range	UK/Ireland range	
<i>Acridotheres tristis</i>	88	15		Y
<i>Agelaius phoeniceus</i>	2	23		N
<i>Alauda arvensis</i>	704	155	82	Y
<i>Alectoris barbara</i>	15	17		N
<i>Alectoris graeca</i>	362	19		N
<i>Alectoris rufa</i>	19	16	15	N
<i>Alopochen aegyptiacus</i>	8	10		N
<i>Anas acuta</i>	102	14		N
<i>Anas penelope</i>	32	22	17	N
<i>Anser anser</i>	7	14	13	N
<i>Athene noctua</i>	221	74	35	Y
<i>Aythya ferina</i>	9	12		N
<i>Callipepla californica</i>	1133	12		Y
<i>Carduelis cannabina</i>	203	87	56	N
<i>Carduelis carduelis</i>	615	67	24	Y
<i>Carduelis chloris</i>	91	87	63	Y
<i>Carduelis flammea</i>	618	36	11	Y
<i>Carduelis flavirostris</i>	59	65	48	N
<i>Carduelis spinus</i>	54	51	30	N
<i>Corvus frugilegus</i>	102	24	17	Y
<i>Corvus monedula</i>	5	24	15	N
<i>Cygnus olor</i>	29	13	13	Y
<i>Emberiza cirrus</i>	11	15	11	Y
<i>Emberiza citrinella</i>	620	115	81	Y
<i>Emberiza schoeniclus</i>	11	45	42	N
<i>Erethacus rubecula</i>	81	148	144	N
<i>Fringilla coelebs</i>	354	304	259	Y
<i>Fringilla montifringilla</i>	120	34	27	N
<i>Lagopus lagopus</i>	4	61	55	N
<i>Lullula arborea</i>	5	18		N
<i>Passer domesticus</i>	307	202	97	Y
<i>Passer montanus</i>	14	49		N
<i>Pavo cristatus</i>	2	11		Y
<i>Perdix perdix</i>	467	47	23	N
<i>Phasianus colchicus</i>	244	41	25	Y
<i>Prunella modularis</i>	404	106	102	Y
<i>Pyrrhula pyrrhula</i>	2	46	37	N
<i>Sturnus vulgaris</i>	701	252	210	Y
<i>Sylvia atricapilla</i>	5	17		N
<i>Sylvia communis</i>	2	51	32	N
<i>Tetrao tetrix</i>	13	12		N
<i>Turdus merula</i>	785	149	109	Y
<i>Turdus philomelos</i>	577	94	84	Y
<i>Tyto alba</i>	7	15		N
<i>Vanellus vanellus</i>	124	52	48	N

Table 1 The number of host individuals that were introduced to New Zealand (Veltman *et al.* 1996; Duncan 1997; Duncan *et al.* 1999); and the number of host individuals that were sampled by Meinertzhagen in the host species' global range (excluding New Zealand) and UK/Ireland range

To determine whether the parasites recorded on host species in their native range were present on the same host species in New Zealand, we compiled a list of the chewing louse species recorded on 36 introduced bird species in New Zealand from collections at the Museum of New Zealand Te Papa Tongarewa and the Natural History

Museum (London, UK), and from the published literature (primarily Pilgrim & Palma 1982; Palma 1999). We supplemented these records with data from our own field sampling of 404 host individuals of 15 introduced species collected throughout New Zealand. We sampled for chewing lice by dust-ruffling live birds (primarily passerine

species; Clayton & Drown 2001) and washing dead birds (Galloway 2005).

Our datasets included host species from the five main Orders introduced to New Zealand (Passeriformes, Strigiformes, Galliformes, Anseriformes and Ciconiiformes; Appendix S5). Only a few host species were introduced from most other Orders, and these tended to be excluded from our analyses due to insufficient host data (i.e. information on the numbers of the host individuals introduced) or parasite data. The only notable exclusion was the Columbiformes, of which nine host species were introduced to New Zealand.

Missing the boat

To estimate the probability that a parasite genus or species 'missed the boat', we used data on the size of host founding populations in New Zealand along with data on the pattern of parasite infection in the global and UK/Ireland datasets to simulate host arrival. Each simulation involved selecting at random (with replacement) a number of host individuals of each species from either the global or UK/Ireland datasets equal to the number of host individuals of those species in the New Zealand founding populations (Table 1). From this sample, we then determined which chewing louse genera or species were present in the simulated introduction. We repeated this process 1000 times and, for each chewing louse genus or species, calculated the probability that it missed the boat [$P(\text{MB})$] as the proportion of absences in the 1000 simulations (Appendices S1–S4).

Our analysis assumes that the pattern of parasite infection in the global and UK/Ireland data sets mirrors the infection pattern at those sites where host birds were collected for introduction to New Zealand. However, there may be spatial and temporal heterogeneity in parasite prevalence in host populations in their native ranges that would violate this assumption. Most host individuals introduced to New Zealand were probably captured at locations in the south of England near ports where ships sailed from, but in general the exact location of source populations is rarely reported in the literature. To test for potential sampling bias associated with the geographical location of host populations within the UK, we repeated the random sampling processes using only specimens collected within two locations (Scotland and England) independently to estimate the probability of a parasite species missing the boat in hosts collected from two separate locations. We used a Wilcoxon sign test to test for a significant difference in the average probability of species missing the boat in the two locations.

Sinking with the boat

Many chewing louse genera and species have more than one host species, and for a genus or species to 'sink with the boat'

all of its potential hosts must fail to establish following introduction. For each parasite genus or species, we calculated the probability that its boat sank [$P(\text{BS})$] by calculating the proportion of its potential host species that failed to establish following introduction to New Zealand, using the data in Veltman *et al.* (1996), Duncan (1997) and Duncan *et al.* (1999). However, not all parasites whose boat sank will have sunk with the boat: some parasites whose boat sank may have already failed because they missed the boat. The probability that a parasite sank with the boat [$P(\text{SB})$] is the probability that a parasite did not miss the boat and that its BS [$P(\text{notMB and BS})$]. From the laws of probability, this equates to: $P(\text{SB}) = P(\text{notMB} | \text{BS}) P(\text{BS})$. We calculated $P(\text{notMB} | \text{BS})$ from the simulation results (the probability that a genus or species did not miss the boat for those parasites whose hosts failed to establish) and multiplied this by $P(\text{BS})$ to estimate $P(\text{SB})$.

Lost overboard

In this study, there are only four possible outcomes for a parasite found on an introduced host in the native range: it either missed the boat, boat sank, was lost overboard or succeeded in establishing. We can calculate the probability that a parasite, whose host was introduced, subsequently established in New Zealand [$P(E)$] as the number of parasite genera or species recorded in New Zealand divided by the total number of parasite genera or species recorded on all introduced host species in their native range. As the probabilities of the four possible outcomes must sum to one, we can then calculate the probability that a species was lost overboard as: $P(\text{LO}) = 1 - [P(\text{MB}) + P(\text{SB}) + P(E)]$.

Mechanisms of parasite persistence on successful hosts

For parasites that arrived with their host species, and the host established in New Zealand, there were two outcomes: they either established or failed to persist for other reasons (lost overboard). We investigated three mechanisms that might influence the probability of parasite persistence given arrival and host establishment: 'propagule pressure', with larger founding populations of parasites more likely to persist (Lockwood *et al.* 2005); parasite aggregation, with parasite populations highly aggregated on a few host individuals more prone to stochastic extinction (Poulin 2007); and factors linked to transmission efficiency, with parasites having higher transmission efficiency more likely to persist because higher rates of dispersal can buffer populations from extinction.

We estimated the size of founding parasite populations by multiplying prevalence and intensity of parasite infection in the host source population, and the number of host individuals introduced. Degree of aggregation was estimated

using the variance : mean ratio of parasite infection on host individuals (Shaw & Dobson 1995). Both the size of the founding populations and the degree of aggregation were calculated using the mean prevalence and intensity estimates of infection in the introduced host populations generated from the simulated introduction events.

The factors predicted to influence parasite transmission efficiency were parasite host-specificity, host longevity, the number of host individuals introduced and the degree of social interaction among host individuals (Gill 1990; Ewald 1994; Rózsa 1997; Rózsa *et al.* 1996; Rékási *et al.* 1997; Paterson *et al.* 1999, 2003). With the exception of very few stragglers, introduced lice have not been detected on native birds in New Zealand, with native bird species having been well-sampled (Pilgrim & Palma 1982; Palma 1999). Hence we used an index of host-specificity equalling the number of potential host species that were successfully introduced to New Zealand, for a particular chewing louse genus or species (recorded in the global and UK/Ireland datasets respectively), with a lower score indicating higher host-specificity.

We classified lice genera or species according to their suborder (1, Ischnocera; 2, Amblycera). This was included as a transmission efficiency variable since, although both suborders generally require direct contact between hosts for dispersal (the main route of transmission is thus 'vertical' from parents to offspring), a key functional difference between the two suborders is that Amblycera are more vagile than Ischnocera (Marshall 1981). Host body mass was used as a surrogate for host longevity (Reich 2001), and the degree of social interaction between individuals of host species was categorized on a scale of 1–5: 1, solitary or in pairs throughout the year; 2, breed in pairs and in small groups in winter; 3, in groups throughout the year; 4, breed

in pairs and flock in winter; and 5, breed in colonies and flock in winter. We calculated weighted means of host body size and social interaction index for each dataset, taking into account host species composition and founder host population sizes.

We investigated the relative influence of parasite founding population size, aggregation and transmission on parasite persistence (given arrival and host establishment) at the species-level only, as there were insufficient data at the genus-level. Generalized linear models were fitted to subsets of both the global and UK/Ireland datasets in turn, comprising those parasites for which at least one host species established in New Zealand, specifying binomial errors and a logit link because the response variable was binary (persisted = 1, failed to persist = 0). We used a model selection approach to identify the best fitting model or subset of models from a candidate set (Table 2), using Akaike's Information Criterion corrected for small sample sizes (AICc) and AIC weights to compare models (Burnham & Anderson 2002). A conservative threshold of four units for delta AICc difference was used (as opposed to the usual two units) as some candidate models added more than one parameter. To allow for the probability that some parasites may have failed to persist because they missed the boat, rather than being lost overboard, we weighted observations in each model by their probability of having not missed the boat [weight = $1 - P(\text{MB})$]. Founding population size, the number of host individuals and host body size were log-transformed. All explanatory variables, except parasite suborder, were centred and standardized using the formula $(x - \text{mean})/\text{SD}$. We calculated the model-averaged parameter estimates and estimates of unconditional standard errors using information from the full set of models (see eqns 4.1 and 4.9 in Burnham & Anderson 2002). Approximate

Table 2 Candidate models fitted to the observed parasite species data and best set of models identified by the model selection (highlighted in bold, based on ΔAICc threshold value < 4) for the global and UK/Ireland datasets

Model	Hypothesis	d.f.	Global				UK/Ireland			
			AICc	ΔAICc	AIC weight	AUC	AICc	ΔAICc	AIC weight	AUC
m5	Propagule pressure + transmission efficiency	7	63.8	0	0.43	0.855	39.1	0.2	0.37	0.93
m3	Transmission efficiency	6	65.0	1.2	0.24	0.887	38.9	0	0.42	0.93
m7	Propagule pressure + aggregation + transmission efficiency	8	65.5	1.7	0.19	0.860	41.7	2.9	0.10	0.93
m6	Aggregation + transmission efficiency	7	67.0	3.3	0.09	0.885	41.4	2.5	0.12	0.93
m1	Propagule pressure	2	68.2	4.4	0.05	0.741	55.2	16.3	0	0.74
m4	Propagule pressure + aggregation	3	71.1	7.3	0.01	0.715	56.0	17.1	0	0.76
m0	Null	1	76.6	12.9	0.00	0.500	57.7	18.8	0	0.50
m2	Aggregation	2	78.2	14.4	0.00	0.728	58.6	19.7	0	0.79

'Transmission efficiency' included five factors predicted to influence parasite transmission efficiency (see Methods): the host founder population size, host body mass, host sociality, the degree of host specificity and parasite suborder. AUC (area under receiver operator curve) values were used to assess model performance (see Methods) following the guidelines of Hosmer & Lemeshow (2000): $0.7 \leq \text{AUC} < 0.8$ = acceptable; $0.8 \leq \text{AUC} < 0.9$ = excellent; $0.9 \leq \text{AUC}$ = outstanding.

95% confidence intervals for parameter estimates were calculated using two times the standard error estimates.

Model performance was assessed by calculating the area under the receiver operating curve (AUC). In the present context, AUC measures the likelihood that a parasite species which failed to persist will have a higher predicted probability of failure from the model than a species that persisted. An AUC value of 0.5 indicates a model that performs no better than chance, while AUC values closer to one indicate models that more accurately assign probabilities (Hosmer & Lemeshow 2000).

All analyses were carried out using the statistical package R (v2.9.2; <http://www.r-project.org>; R Development Core Team 2009). AUC values were calculated using the ROCR package (Sing *et al.* 2005).

RESULTS

Proportion of parasites lost

At the genus-level, the total number of parasites recorded on host study species in their native range was similar in both the global (30 genera) and UK/Ireland (28 genera) datasets (Fig. 1a; Appendices S1 and S2); however, at the species-level the number was much higher in the global dataset (109 species) than in UK/Ireland (64 species; Fig. 1b; Appendices S3 and S4). Forty per cent of parasite genera recorded on hosts in the native range were absent from New Zealand (global: 40%; UK/Ireland: 39%), as were approximately two-thirds of parasite species (global: 70%; UK/Ireland: 62%).

Causes of parasite loss

Figure 1 shows our estimates of the proportion of parasite genera and species lost through missing the boat, sinking with the boat or being lost overboard for both the global and UK/Ireland datasets. Two general patterns emerge. First, most parasite genera and species failed by sinking with the boat, followed by being lost overboard, with a smaller proportion having missed the boat. Second, the proportional losses were greater at the species-level than at the genus-level. Overall, the probability of parasite establishment was similar for the global and UK/Ireland datasets.

Within the UK, the probability of missing the boat for parasite species was similar irrespective of the location of the source population (England vs. Scotland; Wilcoxon test: $W = 856.5$, $P = 0.953$).

Mechanisms of parasite loss given arrival and host establishment

Twenty parasite genera were recorded on host species that were successfully introduced to New Zealand in both the

global and UK/Ireland datasets (Fig. 2a), but more parasites were recorded at the species-level in the global dataset (58 species) than in the UK/Ireland one (41 species; Fig. 2b). For parasites whose hosts established in New Zealand, 15% were absent from New Zealand at the genus-level compared with *c.* 42% at the species-level for both datasets, with the probability of being lost overboard much higher than the probability of having missed the boat in all cases (Fig. 2).

Model selection failed to identify a single best-fit model for either the global or UK/Ireland datasets. Greatest support (as determined by the AICc values and Akaike weights) was given to the same four models for both datasets, with transmission efficiency present in all four models (Table 2). While propagule pressure and aggregation were also present in two models each, the model-averaged parameter estimates for these two variables were not clearly different from zero (Fig. 3). In contrast, parameter estimates of variables associated with transmission efficiency were clear predictors of parasite persistence. Persistence was positively associated with host body mass, and more likely for Ischnocera than for Amblycera, in both datasets, and positively associated with host founder population size in the UK/Ireland dataset. There was also a trend of a negative association between host sociality and parasite persistence in the UK/Ireland dataset. AUC values indicate that model performance was acceptable or excellent for all models except the null model, which performed no better than chance (Table 2).

DISCUSSION

The hypothesis that sorting events lead to parasite species loss upon host introduction to, or invasion of, a new locality was supported by our data showing that a high proportion of ectoparasitic chewing lice (40% of genera and > 60% of species) were lost from their avian hosts upon introduction to New Zealand. The trend for lower parasite loss at the genus than the species-level is not surprising given that a particular genus may encompass more than one parasite species (i.e. it has more 'chances' of successful introduction), and parasite genera typically have representation on more host species (i.e. do not have 'all of their passengers in one boat', as is the case for host-specific parasite species). The genus level analyses are therefore a relatively conservative assessment of parasite loss, but they do indicate that parasite loss is a general phenomenon among the chewing lice, rather than being limited to a subset of genera.

Processes of parasite loss

We demonstrate for the first time for any group of parasites that relatively few chewing lice species on birds introduced to New Zealand would have 'missed the boat', but a high

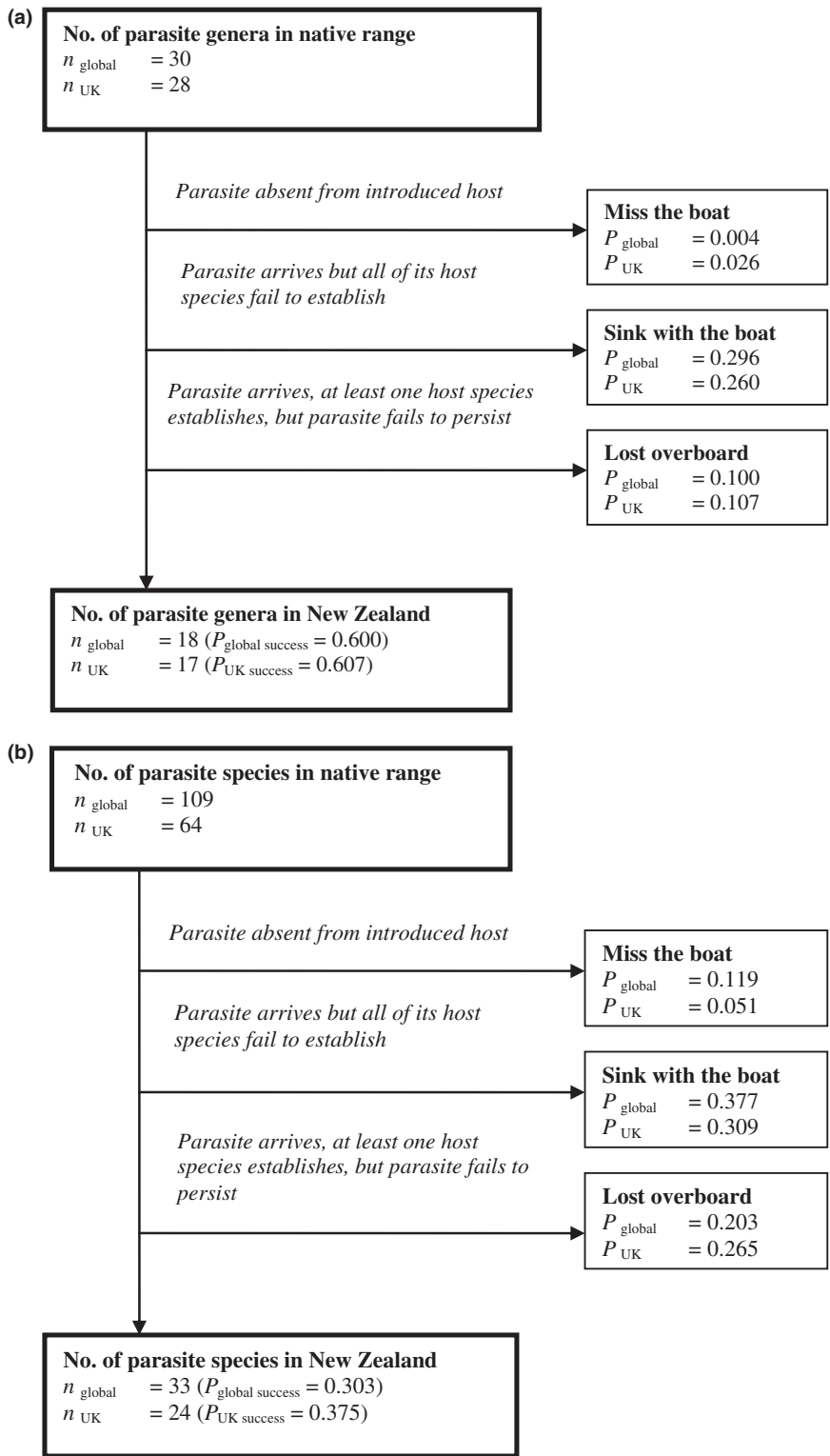


Figure 1 Probability of parasite loss at three different stages in the introduction process for the genera and species levels for two datasets (global and UK/Ireland).

proportion would have ‘sank with the boat’ or been ‘lost overboard’. In other words, chewing louse species would rarely have been absent from their avian host species upon

introduction to New Zealand, but they had a relatively high chance of failure because their hosts or the parasites themselves failed to establish populations in their new

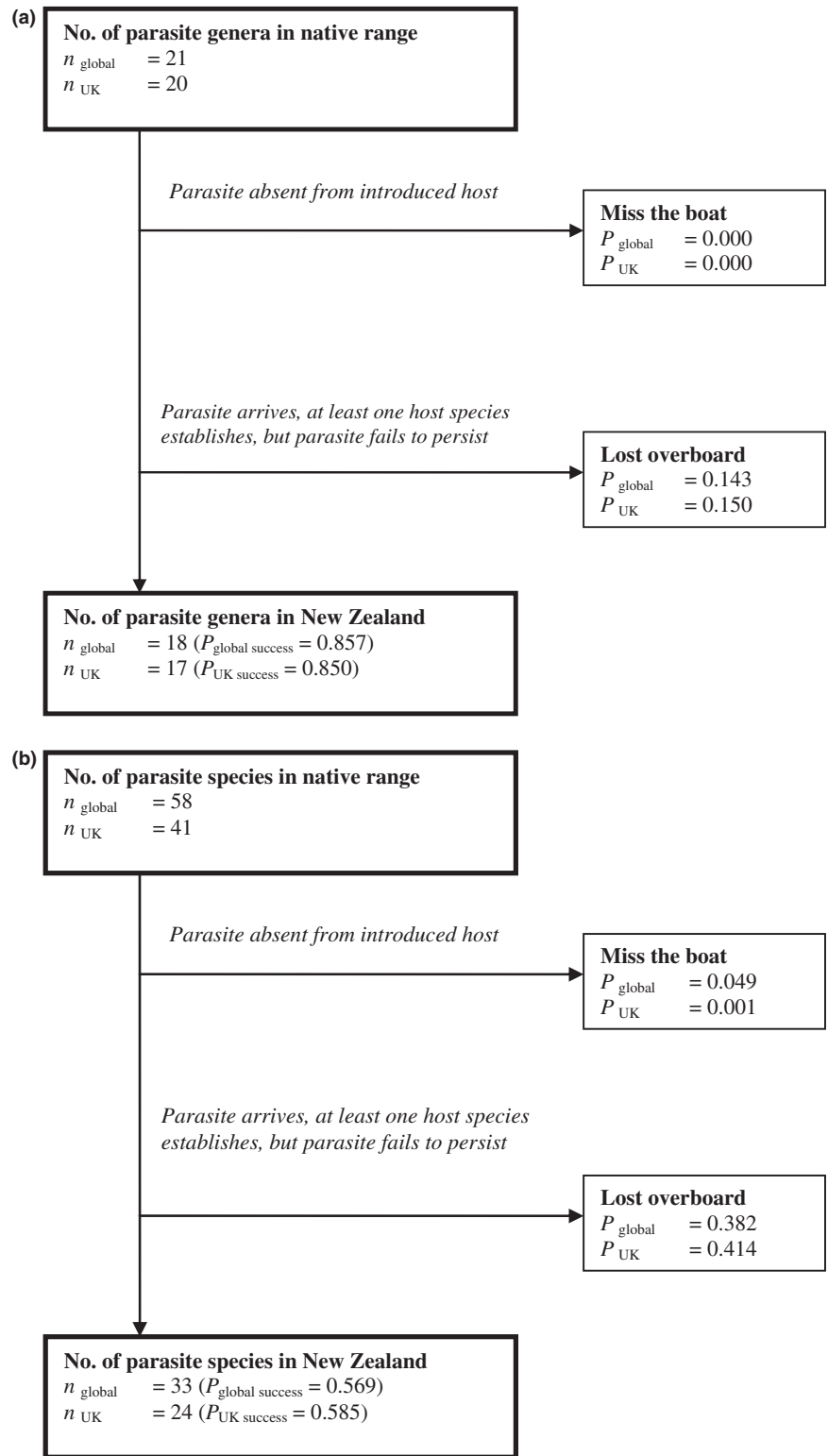


Figure 2 Probability of failure for parasites with at least one host species successfully introduced to the new environment.

environment. This pattern was broadly consistent across the subsets of data considered from different geographical locations and taxonomic groups, indicating that these results

apply under a range of different conditions. Hence, there was no evidence of an important influence of environmental variables on the probability of louse persistence. That

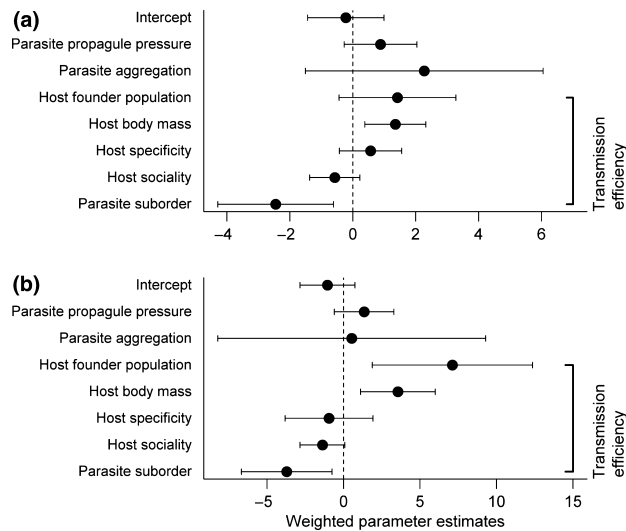


Figure 3 Model-averaged parameter estimates (\pm 95% confidence interval) predicting persistence for parasite species with at least one host species successfully introduced to its new environment, using data from the: (a) global and (b) UK/Ireland datasets. (Parasite suborder is a factor, where 1 = *Ischnocera* and 2 = *Amblycera*.)

parasite species in the global dataset were more likely to fail due to missing the boat, compared with those in the UK/Ireland dataset, probably reflects that introduced host individuals would have been sourced from only parts of their global ranges, and thus many parasite species with restricted geographical ranges would have had no chance of being included in the host sample.

The relative importance of 'sinking with the boat' and being 'lost overboard', in determining parasite loss, varied between analyses. 'Sinking with the boat' accounted for the loss of approximately a third of parasite species and a quarter of parasite genera upon introduction to a new environment, while being 'lost overboard' accounted for the loss of at least 20% of species but only 10% of genera. This pattern can again be accounted for by parasite genera having more chances of successful introduction than parasite species, with the effect of this being less on the probability of the parasite having at least one host persisting at the new location, than on the probability of the parasite itself persisting. This indicates that improved establishment success at the genus-level is more a product of having multiple chances, than having broader host ranges.

Reassuringly, with respect to 'sinking with the boat' or being 'lost overboard', there was little variation in the relative importance of factors between the global and UK/Ireland datasets. The one difference observed, at the species-level, is that parasites in the global dataset were more likely to 'sink with the boat' than those in the UK/Ireland dataset. This trend can be explained by

differences in patterns of host persistence between datasets. Previous studies have shown that host species introduced to New Zealand from the UK were more likely to establish populations in their new range than host species introduced from outside the UK (Duncan *et al.* 1999). In other words, a high proportion of parasites in the global dataset failed to persist in their new environment, simply because none of their potential host species were successfully introduced. Thus, the processes influencing host persistence upon introduction to a new environment (e.g. Blackburn & Duncan 2001; Duncan *et al.* 2003) are also key determinants of parasite persistence. Notably, although there was no evidence of a direct influence of environmental variables on the probability of louse persistence, such variables do influence host establishment (e.g. Duncan *et al.* 2001), and thus may still be important at the 'sinking with the boat' stage of introduction.

Potential sources of bias

Previous studies have raised concerns about the integrity of Meinertzhagen's bird and (to a lesser extent) parasite collections, but we believe these collections provide a valuable resource for addressing the questions set out in this paper. Some bird specimens in Meinertzhagen's collections have been shown to be fraudulent (e.g. Knox 1993; Rasmussen & Prÿs-Jones 2003; Kennerley & Prÿs-Jones 2006) but these relate primarily to new (and extreme) vagrant records for a few particularly rare species, generally in Asia. The risk of fraudulent geographical locations for host specimens being included in our analysis is negligible because: (1) we examined parasite infection in relatively common species whose distributions are well known; (2) we used very broad measures of the hosts' geographical range (global and UK/Ireland) and (3) we excluded rare hosts by analysing only species with at least ten host specimens sampled for parasites. The risk of fraudulent parasite specimens being included in our analyses is also negligible because we could cross-reference to the actual collections. In addition, louse specimen records that could not be identified to the species or genus-level, or were not included in the relevant world or UK species check-lists, were retained according to a higher (and therefore more conservative) taxonomic classification.

The probability of a parasite missing the boat may vary if parasite prevalence varies spatially and temporally within their host populations, but the exact location that host individuals were sourced for introduction to New Zealand was rarely reported. Our analyses show, however, that the probability of missing the boat was similar for two geographical locations within the UK (i.e. England and Scotland), giving some confidence that our results for

missing the boat are not affected by heterogeneity in source population parasite prevalence.

Although the main orders of host species introduced to New Zealand were included in our analyses, species from some orders were excluded due to missing data on either host introduction effort or parasite infection rates. The host species that were excluded due to missing data on introduction effort probably had low rates of introduction and were more likely to fail to establish in New Zealand than those included in our analyses (Veltman *et al.* 1996; Duncan 1997), implying that we may have underestimated the probability of sinking with the boat.

An additional potential source of bias was whether the birds released in New Zealand were randomly selected individuals or specifically chosen high-quality individuals with low parasite loads. Our analysis assumes the former, but if high-quality individuals were selected then we will have underestimated the probability of missing the boat. Similarly, at the lost overboard stage, we are unable to determine whether parasite loss may have occurred during transportation to New Zealand or following host introduction, or whether the process of transportation made some parasite species more or less likely to fail on arrival in New Zealand. Once parasites were onboard, these processes would have contributed to being 'lost overboard'.

Mechanisms of parasite loss on successful hosts

The rate of, and mechanisms determining, parasite loss from successfully introduced hosts is of particular interest because hosts that escape regulation from their parasites often become significant pests (Keane & Crawley 2002). Our analysis shows that *c.* 40% of the parasite species considered here, and 15% of the genera, were lost from the subset of successfully introduced host species. For all datasets (global and UK/Ireland) and taxonomic levels (species and genera), most parasites were lost overboard, rather than missed the boat. Hence, most parasites were introduced to the new environment but a relatively high proportion failed to persist once introduced. To understand the risk of host release from enemy regulation, we need to understand the importance of the different potential mechanisms determining parasite persistence in the new environment.

We investigated the relative importance of three mechanisms (parasite propagule pressure, aggregation and transmission efficiency) in parasite persistence (i.e. the probability of not being 'lost overboard') at the species-level. Only transmission efficiency consistently emerged as an important mechanism, as this was the only factor included in all of the best-fit statistical models, and the only one with model-averaged parameter estimates clearly different from zero, for both the global and UK/Ireland datasets.

In line with our predictions, parasite persistence was positively associated with host body mass (as a surrogate for host longevity) and, for the UK/Ireland dataset, the number of host individuals introduced (both factors believed to facilitate efficient parasite transmission). However, contrary to our predictions, Amblyceran as opposed to Ischnoceran parasites, and possibly those associated with more social hosts (both factors again believed to facilitate efficient parasite transmission), had a lower chance of persisting in their new environment. It may be that less vagile parasites, or those on less social hosts, may persist better in the phase of disrupted transmission at low host population densities, such as following initial introduction to a new environment. For example, at low host population density, a parasite more likely to wander off its host would be less likely to survive than one that stayed put. Alternatively, for the parasite suborder effect, other life-history trait differences may over-ride any influence of vagility.

CONCLUSIONS

Using bird introductions and their associated ectoparasitic chewing lice, this study demonstrates that very few parasites were absent from their host founder populations (i.e. missed the boat). Instead, most parasites failed because hosts failed to establish (sank with the boat), implying that the processes determining host introduction success are key to parasite establishment. For parasites with an established host population many (40% of species and 15% of genera) failed to persist in their new environment (i.e. were lost overboard), with parasite persistence influenced by transmission efficiency (large host body size, large host founder population size, parasite suborder and, possibly, low host sociality) rather than parasite propagule pressure and aggregation.

The approach outlined in this study is equally applicable to other parasite groups and their hosts, but contingent on the availability of suitable data. Insights gleaned from such analyses should facilitate in both understanding and managing the impact of both host and parasite introductions to new environments.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Chewing lice genera (taxonomy follows Price *et al.* 2003) introduced to New Zealand (NZ). Chewing lice

founder population parameter estimates are based on information collected from the host specimens sampled anywhere in their global range (excluding New Zealand).

Appendix S2 Chewing lice genera (taxonomy follows Price *et al.* 2003) introduced to New Zealand (NZ). Chewing lice founder population parameter estimates are based on information collected from the host specimens sampled anywhere in the United Kingdom or Ireland.

Appendix S3 Chewing lice species (taxonomy follows Price *et al.* 2003) introduced to New Zealand (NZ). Chewing lice founder population parameter estimates are based on information collected from the host specimens sampled anywhere in their global range (excluding New Zealand).

Appendix S4 Chewing lice species (taxonomy follows Price *et al.* 2003) introduced to New Zealand (NZ). Chewing lice founder population parameter estimates are based on information collected from the host specimens sampled anywhere in the United Kingdom or Ireland.

Appendix S5 Summary of the number of host species excluded from and included in the analyses in relation to host taxonomy (order) within the global and UK/Ireland datasets.

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